

SPATIAL PROPERTIES OF NICHE SEPARATION AMONG  
*EUEIDES* AND *DRYAS* BUTTERFLIES (LEPIDOPTERA:  
NYMPHALIDAE: HELICONIINAE) IN COSTA RICA

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*Abstract.*—Young, Allen M., Invertebrate Division, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.—Habitat and larval food plant associations of heliconiine butterflies (Lepidoptera: Nymphalidae), *Dryas iulia* (Fabricius), *Eueides lybia* (Fabricius), *E. aliphera* (Godart), and *E. isabella* (Cramer) were examined briefly in three regions of northern Costa Rica. The following patterns were found: (1) although *E. lybia* and *E. aliphera* are sympatric and utilize the same larval food plant, *Passiflora vitifolia* H.B.K. (Passifloraceae) in tropical wet forest, they are not micro-sympatric since the former occurs along shaded forest edges and forest light gaps, while the latter occurs in open secondary habitats; (2) *Dryas iulia* is sympatric with both species (1) and it is microsympatric with *E. aliphera* but uses a different larval food plant, *P. auriculata* H.B.K.; (3) both *D. iulia* and *E. isabella* are microsympatric in the Meseta Central and use both the same larval food plant (*P. adenopoda* D.C.) and nectar source (*Serjania* cf. *atrolineata* Saw. & Wright—Sapindaceae) during the dry season; (4) in a patch of semi-deciduous forest in the lowland tropical dry forest zone, *D. iulia* shares a larval food plant, *P. capsularis* L., with *E. isabella*, but also uses *P. platyloba* Killip and *P. suberosa* Juss. The widespread occurrence of *D. iulia* may be due to a high tolerance for heat and low humidity, and the use of *Plectostemma* subgenus of *Passiflora* as food plants. Other factors, such as oviposition behavior and larval habits, are also discussed.

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The heliconiine butterfly *Dryas iulia* (Fabricius) (Lepidoptera: Nymphalidae: Heliconiinae) is widespread in tropical wet and dry forest regions of Costa Rica. Emsley (1963) points out that it is very widespread throughout much of subtropical and tropical America. In some regions of Costa Rica, it is sympatric with at least two or three species of another heliconiine genus, *Eueides*. Adults of one of these, *E. aliphera* (Godart), are strikingly similar to *D. iulia*, and the two heliconiines often occur together (Emsley, 1963). *Eueides aliphera* is also often sympatric with *E. lybia* (Fabricius) and *E. isabella* (Cramer) in the tropical wet forests of northeastern Costa Rica. Although the life cycles and larval food plant associations of these butterflies (Figs. 1 and 2) are known from various regions of tropical America (Beebe et al., 1960; Alexander, 1961a, b; Brown and Mielke, 1972;



Fig. 1. *Dryas iulia* (Fabricius), *Eueides aliphera* (Fabricius), and *E. lybia* (Fabricius) from "Tirimbina," near La Virgen de Sarapiquí, Heredia Province, Costa Rica. These individuals were reared from the egg stage.



Fig. 2. *Eueides isabella* (Cramer) from San Rafael de Ojo de Agua, Alajuela Province, Costa Rica. *Eueides aliphera* trapped in spider web at "Tirimbina" (February 1977).

Benson et al., 1976), this paper reports some aspects of niche separation in three regions of northern Costa Rica: (1) Meseta Central, where *D. iulia* occurs with *E. isabella*, (2) northeastern premontane tropical wet forest where *D. iulia* occurs with *E. lybia* and *E. aliphera*, and (3) a patch of semi-deciduous forest in the tropical dry forest zone, Puntarenas Province, where *D. iulia* occurs with *E. isabella*. The general thesis explored by these descriptive field observations is that co-occurring heliconiines may exhibit niche differences, and these patterns may vary regionally.

### Methods

During the period of 25 July–27 August 1976, the habitat, life cycle, and larval food plants of *E. lybia* were studied at "Tirimбина," La Virgen, Heredia Province, a region of Premontane Tropical Wet Forest (Holdridge, 1967), and *E. isabella* was similarly studied at the "Barranca Site," a small semi-deciduous forest in Puntarenas Province (see Orians, 1969 for description of this locality). *Eueides isabella* was again studied from 15 January–23 February 1977 but at San Rafael de Ojo de Agua, Alajuela Province, in Tropical Moist Forest (Holdridge, 1967) of the Meseta Central. *Eueides aliphera* was studied at "Tirimбина," 12 January–18 February 1977. *Dryas iulia* was studied as follows: (1) 3 February–14 March 1977—"Tirimбина," with rearing continuing in Milwaukee, Wisconsin (3–14 March); (2) 15 January–23 February 1977—San Rafael de Ojo de Agua; (3) 25 January and 24 February 1977—Barranca Site. Observations were made on: nectar sources, larval food plants (including oviposition), and behavior of immature stages. Occasionally, a few individuals of each species were reared, using previously developed techniques (Young, 1975, 1976).

### Results

Although *E. isabella* occurs in northeastern Costa Rica (e.g., at "Finca La Selva," Puerto Viejo, pers. obs.), it was not seen at "Tirimбина" during the study periods, but habitat differences were seen here for *E. lybia* and *E. aliphera*. *Eueides lybia* adults are most commonly seen along the edges of shaded primary forest and forest light gaps (tree fall areas). The life cycle (Fig. 3) takes place on *Passiflora vitifolia* H.B.K. (Passifloraceae), a large forest vine. Population numbers of *E. lybia* are generally low, and adults are concentrated near certain individuals of *P. vitifolia*. A fresh female *E. lybia* shows up several times daily to lay eggs. Within a 10-minute period, as many as 12 eggs can be deposited on a vine, usually one per leaf. The white egg is deposited on the under side of an old leaf after considerable inspection of the vine. Daily observations indicate that adult populations are confined to small areas of preferred habitats.

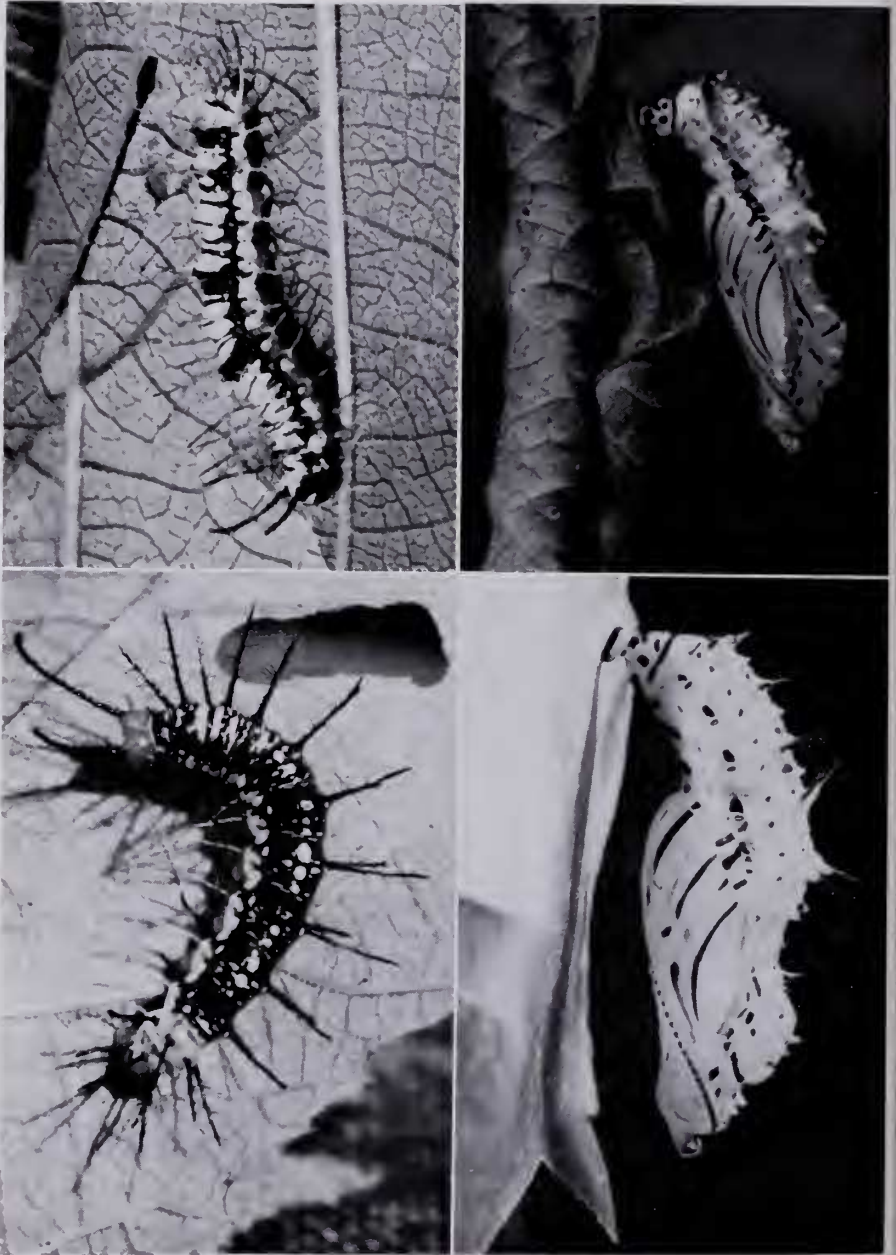


Fig. 3. Top: fifth instar larva and pupa of *E. aliphera*; bottom: same for *E. lybia*. Both series from "Tirimbina."



Fig. 4. Cut-over forest habitat at "Tirimbina" where young vines of *P. vitifolia* are abundant in direct sunlight and used for oviposition by *E. aliphera* (February 1977).

In open secondary vegetation, *E. aliphera* is very abundant and adults generally stay closer to the ground than seen for *E. lybia*. Oviposition takes place on small, tender *P. vitifolia* vines. A major habitat of *E. aliphera* at "Tirimbina" is recently cut-over forest, where young *P. vitifolia* grow over logs and branches of fallen trees (Fig. 4). The larva and pupa of *E. aliphera* and *E. lybia* are strikingly similar in appearance (Fig. 3) and size. The major distinction between the two species is the habitat: *E. aliphera* prefers low vegetation exposed to direct sunlight while *E. lybia* prefers shaded forest edges and light gaps (where indirect sunlight is filtered down from the canopy). Oviposition by *E. aliphera* is similar to *E. lybia* but egg production might be higher in the former: one fresh female on 12 January 1977 deposited 27 eggs on an isolated small vine of *P. vitifolia* within a 10-minute period at 11:00 AM. This vine was then inspected on three dates before the end of the month, and within 15 days only three larvae (third instars) were left. Unlike *E. lybia*, several eggs were deposited on a single leaf, although other leaves were also used the same day. Adult populations of *E. aliphera* are large and fluid, being distributed over a large area. Small clumps of *P. vitifolia* occur over small areas.

During the intense dry season of the Meseta Central, flowering shrubs



Fig. 5. Stream-edge forest remnant at San Rafael de Ojo de Agua where *E. isabella* and *D. iulia* are abundant during the pronounced dry season of this region, and where a nectar source, *Serjania* cf. *atrolineata* (Sapindaceae) and larval food plant, *Passiflora adenopoda* attract the butterflies at this time.

and trees along streams attract many butterflies, and *E. isabella* shows up at flowering bushes of *Serjania* cf. *atrolineata* Saw. & Wright (Sapindaceae) (Fig. 5). An example is San Rafael de Ojo de Agua, where *E. isabella* visits the inflorescences (Fig. 6) along with *D. iulia* and several other butterflies (mostly Nymphalidae and Pieridae). One particular bush that was frequently visited by *E. isabella* and *D. iulia* was situated about three meters from a large vine of *Passiflora adenopoda* H.B.K. (Fig. 7), where oviposition by both was observed. Inspection of the vine on several dates (January–February 1977) turned up many eggs and larvae of *E. isabella* and a few of *D. iulia*. The egg of *E. isabella* is deposited singly on the under side of an old leaf, and occasionally eggs were deposited on branches of bamboo that intertwined with the food plant. Oviposition by *E. isabella* is a very time-consuming process with a lot of time spent in “false” oviposition acts at the food plant. The larva bears a very close general resemblance to those of the other *Eueides* studied, but the pupa is distinct (Fig. 8). In comparison to *E. lybia* and *E. aliphera*, *E. isabella* exhibits several differences: (1) different strategy of wing color pattern; (2) different larval



Fig. 6. *Eueides isabella* visiting inflorescence of *S. cf. atrolineata* at 1:00 PM 15 January 1977 at San Rafael de Ojo de Agua.





Fig. 7. *Passiflora adenopoda*, a larval food plant of *D. iulia* and *E. isabella* at San Rafael de Ojo de Agua. Note large woody tendrils.

food plant; (3) more pronounced divergence of the pupa stage. Like *E. aliphera* the preferred habitat of this species during the dry season is the open stream-edge exposed to direct sunlight. At this time of the year, adults are concentrated near a nectar source and breeding takes place nearby. During the wet season at the Barranca Site near the Pacific coast, *E. isabella* is abundant in the drier areas of the forest where *P. platyloba* Killip is found; eggs and larvae have been found on this vine. During the dry season this butterfly is scarce or absent here.

*Dryas iulia* is abundant at "Tirimbina" in open secondary vegetation where a larval food plant, *P. auriculata* H.B.K. (Fig. 9) grows in small patches heavily intertwined with, and shaded by, other vines. Unlike *P. vitifolia*, this vine has very smooth leaves and woody tendrils. A second food plant species of *D. iulia* here, *P. biflora* D.C., also has smooth leaves and woody tendrils. Both vines grow in the same habitat as *P. vitifolia*. Here, *E. aliphera* and *D. iulia* fly together. The egg is deposited on a woody tendril, which also functions as a perch for the first instar larva; older larvae rest on leaves and pupation sometimes occurs on the food plant (Fig. 10). Like *E. aliphera*, *D. iulia* is very abundant and the adults are dispersed over large areas. When a female shows up at a vine, she may deposit 2 or 3 eggs on different tendrils within two minutes; the large bright yellow egg is very conspicuous against the shaded back-



Fig. 8. Life stages of *E. isabella* from San Rafael de Ojo de Agua: egg, third instar larva, fifth instar larva and pupa.

ground of the surrounding vegetation. On two days (3 and 8 February 1977) a very frayed female (probably the same individual) showed up at a young vine of *P. biflora* at about 1:00 PM depositing two eggs on the first date and one on the second date. The eggs are invariably deposited



Fig. 9. *Passiflora auriculata*, a larval food plant of *D. iulia* at "Tirimbina."

on vines in very shady conditions; when a larva is placed in sunlight, it becomes very agitated and starts to move very rapidly.

Like the food plants of *D. iulia* at "Tirimbina," the food plant at San Rafael de Ojo de Agua, *P. adenopoda*, possesses woody tendrils. At the Barranca Site, at least three species of *Passiflora*, all with woody tendrils and smooth leaves, are used as food plants by *D. iulia*: *P. aff. capsularis*



Fig. 10. Pupa and fifth instar larva of *D. iulia* (see also excellent diagrams in Beebe et al., 1960). Note woody tendril of *P. auriculata* in both photographs.

L., *P. platyloba* Killip, and *P. suberosa* Juss. (Fig. 11). These vines have fresh leaves during the intense dry season, and two lines of evidence indicate breeding at this time: One pair of freshly-eclosed mating adults was seen (Fig. 12), and the easily-recognizable larval resting perches are common (Fig. 11). Adults are not abundant here at this time. Within a 2 hour period on 24 February 1977, one fresh and three very worn adults of *D. iulia* were seen (1-4 PM). While the *Passiflora* "sub-community" remains lush at this time, *D. iulia*, and perhaps to the exclusion of other sympatric heliconiines, is the only species breeding, perhaps at greatly reduced numbers. Even though some of the vines are very small, they show signs of larval damage from *D. iulia* (Fig. 11). Estimates of developmental times are given in Table 1 and, as expected, they are similar.



Fig. 11. Three larval food plants of *D. iulia* at the "Barranca Site," Puntarenas, Puntarenas Province, Costa Rica, February 1977. Photographs taken in the wild. Top to bottom: *P. platyloba*, *P. aff. capsularis*, and *P. suberosa*. Leaf damage of *P. suberosa* shows larval perching site and pattern of feeding, very characteristic of *D. iulia* (see also Alexander, 1961a). All three vines less than one meter long.



Fig. 12. Mating pair of freshly-eclosed *D. iulia* at the "Barranca Site," 25 January 1977, 11:00 AM. Resting near ground on woody plant.

Table 1. Developmental time\* for the heliconiine butterflies *Dryas iulia*, *Eucides aliphera*, *E. lybia*, and *E. isabella*.\*\*

| Duration of Life Stages (Days): |       |       |       | Larval Food Plant                   |
|---------------------------------|-------|-------|-------|-------------------------------------|
| Egg                             | Larva | Pupa  | Total |                                     |
|                                 |       |       |       | <i>Dryas iulia</i>                  |
| 5                               | 20-21 | 13-14 | 38-40 | <i>Passiflora auriculata</i> H.B.K. |
|                                 |       |       |       | <i>Eucides aliphera</i>             |
| 5                               | 18-19 | 10-11 | 33-35 | <i>P. vitifolia</i>                 |
|                                 |       |       |       | <i>E. lybia</i>                     |
| 5                               | 20-21 | 8     | 33-34 | <i>P. vitifolia</i>                 |
|                                 |       |       |       | <i>E. isabella</i>                  |
| 5                               | 21-22 | 9-10  | 35-36 | <i>P. adenopoda</i> D.C.            |

\* Range of individuals reared was 3-11 and all species were reared in same manner and under similar conditions.

\*\* *D. iulia*, *E. aliphera* and *E. lybia* reared from "Tirimбина" and *E. isabella* from San Rafael de Ojo de Agua (see text).

## Discussion

The phylogenetic affinities of *Eueides* and *Dryas* within heliconiine evolution have been discussed (Emsley, 1965) and their life stages described (Beebe et al., 1960; Alexander, 1961a, b). Unlike some *Heliconius*, which are noted for pollen-feeding (Gilbert, 1972), heliconiines such as *Eueides* and *Dryas*, are nectar-feeders and the distributions of adult populations in space and time must be regulated in part by the availability of the appropriate inflorescences. For example, although many adults of *E. isabella* were found on or near the blooming *Serjania* bush on 15 and 16 January 1977, the blooms were gone by 25 January and no adults were seen in the vicinity, despite an abundance of larval food plant nearby. The persistence and predictability of preferred nectar sources may be a major factor in determining the spatial aspects of adult population structure in heliconiines, perhaps for reasons similar to those discovered for *Heliconius* populations (Ehrlich and Gilbert, 1973; Gilbert, 1975; Cook et al., 1976). In strongly seasonal regions of the tropics, the phenology of flowering might result in a greater mobility of heliconiine populations annually in response to changing distributions of nectar sources. At less seasonal regions such as "Tirimbina," such patterns may be very different.

Different responses and tolerances of butterfly species to environmental parameters such as air temperature may determine where most of the eggs are deposited. Thus although *E. lybia* and *E. aliphera* both use *P. vitifolia* as a larval food plant at "Tirimbina," one species does so most often in one habitat and the other in a different habitat. Perhaps this is a differential response to air temperature and humidity, with one species (*lybia*) being less tolerant of the higher temperatures and lower humidity one presumably finds in open secondary habitats. Such a divergence in niche could lower the probability of local extinctions resulting from interspecific competitive interactions, if larval food plants and nectar sources are limited resources. Selection favors the co-occurrence of *D. iulia* and *E. aliphera* perhaps as a mimicry relationship, although this has not been studied. Brown and Mielke (1972) report that both *E. aliphera* and *E. isabella* have strongly localized populations and that adults tend to stay near the food plants. Cohesiveness of *Eueides* populations is, therefore, predicted to be a result of the distribution of larval food plants and nectar sources, and selection for mimicry with *D. iulia*. The general morphological and color similarity of the larva and pupa between these species suggests another form of mimicry operative in the juvenile stages.

The scarcity or absence of *E. isabella* at "Tirimbina" is surprising since it does occur at other nearby localities. However, as Brown and Mielke (1972) point out, this species is never very abundant locally.

It is generally expected that different heliconiines will have similar de-

developmental times and Beebe et al. (1960) report a generalized heliconiine larval developmental time of about 12 days. The estimates given here are considerably higher. It is likely that food plant differences and other environmental factors will greatly influence this statistic.

Although mortality of eggs and larvae of *D. iulia* is unknown, the observed disappearance of eggs and larvae of *E. aliphera* at "Tirimbina," although limited data, suggest high mortality. Emsley (1963) states that *D. iulia* and *E. aliphera* often share the same habitats. Gilbert (1975) predicts that in general, heliconiine immature stages are killed by ants and other predators. Young (1978) found that eggs and young larvae of *Heliconius hecale* (Fabricius) and *H. cydno* (Bates) disappear at high rates at "Tirimbina," suggesting predation and parasitism. The sophisticated egg-positioning and larval behavior of *D. iulia* (Alexander, 1961a, b; Benson et al., 1976) may offset some mortality. *Eueides* larvae do not exhibit such behavior. *Dryas iulia* sometimes places eggs on plants adjacent to the food plant (Benson et al., 1976) and this may be an effective way of hiding eggs from potential predators (assuming that the larvae can successfully locate the food plant).

Benson et al. (1976) predict that the widespread abundance of *D. iulia* is dependent upon the diversity and abundance of *Plectostemma*, a subgenus of *Passiflora*. *Passiflora adenopoda* is in this subgenus, but at least one other, *P. platyloba*, is in the subgenus *Granadilla* (Benson et al., 1976). Brown and Mielke (1972) report several regional larval food plants of *D. iulia* in Brazil. Of the 42 known larval food plants of about a dozen species of *Eueides*, 34 are in *Granadilla*, and two in *Plectostemma* (Benson et al., 1976). *Passiflora vitifolia* is in the subgenus *Distephana* (Benson et al., 1976). To these considerations it is added that *P. vitifolia* is also used by *Heliconius hecale* and *H. cydno* at "Tirimbina" (Young, 1978). Benson et al. (1976) mention that silvaniform and melpomeniform *Heliconius* radiated mainly onto *Granadilla* and *Distephana*.

The predilection of *D. iulia* for open habitats exposed to direct sunlight and the evergreen condition of the larval food plants are properties that account for the presence of adults during the dry season in lowland Puntarenas Province, a period when other adult heliconiines are noticeably less abundant or absent (pers. obs.). Perhaps *Heliconius* and other heliconiines are less tolerant of dry season conditions here. Another important factor is the availability of preferred nectar sources during the dry season.

The data and above discussion suggest some definite patterns of niche separation for *Eueides* species and *Dryas iulia* in northern Costa Rica that warrant further study. Although *E. lybia* and *E. aliphera* are sympatric in northeastern Costa Rica and utilize the same larval food plant, the former species prefers forest edge habitats and the latter open secondary habi-



tats. The flexibility of the larval food plant for thriving in both types of habitats may be a major factor accounting for this pattern of niche separation between *E. lybia* and *E. aliphera*. *Dryas iulia* occurs in the same habitat as *E. aliphera* but utilizes a different larval food plant species that thrives in shaded undergrowth. At a more seasonal locality, both *E. isabella* and *D. iulia* occur in the same habitat and utilize the same larval food plant and nectar source. In an even more seasonal region, *D. iulia* is sympatric with *E. isabella* and they use the same larval food plant in the same habitat, but at least *D. iulia* has two other food plants there. The widespread occurrence of *D. iulia* over several regions of Costa Rica may be due in part to (1) its ability to use both *Plectostemma* and *Granadilla* larval food plants, and (2) unusually high flexibility in thermal-moisture tolerances.

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